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THE TIFFANY FAUNA, UPPER PALEOCENE

III.—PRIMATES, CARNIVORA, CONDYLARTHRA, AND AMBLYPODA

BY GEORGE GAYLORD SIMPSON

In the first section of this revision, which exigencies of publication have caused to appear as three separate papers, the Tiffany fauna as a whole and its occurrence were reviewed, and the multituberculates, marsupials, insectivores, and a possible bat described. The second section was devoted to the morphology and relationships of *Plesiadapis*, omitting detailed taxonomy. The present paper is the last of this series. It begins with the taxonomy of the Tiffany *Plesiadapis* and completes the review of the fauna.

PRIMATES

PLESIADAPIDAE

PLESIADAPIS GERVAIS, 1877

SYNONYM.—*Nothodectes* Matthew, 1915.

Matthew (1915) based *Nothodectes* on a single fragmentary lower jaw. This did not show any of the striking characters of the *Plesiadapis* group, and comparison with *Plesiadapis* was then possible only through the very inadequate figures of Lemoine, so that the resemblance was not recognized. The discovery of the fine Tiffany material and the publication of better, but still incomplete, figures of the Cernaysian form by Stehlin (1916), led Matthew to recognize the very close resemblance between *Nothodectes* and *Plesiadapis*, and he wrote (1917, p. 832) of the former that "the generic characters do not separate it satisfactorily from *Plesiadapis* as described and figured by Lemoine, but pending a revision of Lemoine's genus it seems better to retain *Nothodectes* provisionally," and he elsewhere noted the possibility that the genera are identical. The principal characters used to distinguish *Nothodectes* provisionally were:

> Upper incisors more elongate and with three, not two, apical cusps.
>
> P^4 with paracone and metacone more separate than usual in *Plesiadapis*.
>
> Upper molars a little less quadrate, with weaker hypocone and external cingulum.

Paraconid less distinct on the lower molars and entoconid shelf of M_3 narrower and more of the normal crested type.

The implication was that these are not primarily generic characters but that they were distinctions indicated by the incomplete evidence available which prevented the assumption of generic identity in the characters not then published for the European species. Teilhard (1921) made the awaited thorough revision of the latter forms and showed that the early species (i.e., those truly of *Plesiadapis* and not of *Platychoerops* in my still more recent usage) do have three lobes on the upper incisor, separate paracone and metacone on P^4, and paraconids much as in *Nothodectes*.[1] He did not specifically mention other points made by Matthew,[2] but as no other distinctions were found, he followed the course indicated by Matthew in such a case and united the genera under the older name, *Plesiadapis*. There can hardly be any question as to the correctness of this synonymy, and it is now generally accepted.

Teilhard also showed that the old generic names *Platychoerops* Charlesworth, 1854, and *Miolophus* Owen, 1865, which are absolute synonyms, refer to an animal closely related to *Plesiadapis* Gervais, 1877. Teilhard considered all three as synonymous,[3] but pointed out that their type species do have very marked distinctions. In 1929 I tabulated these distinctions, pointed out that they are surely of generic rank by ordinary standards, and so accepted both *Platychoerops* and *Plesiadapis* as valid and different genera.[4]

In describing *Plesiadapis cookei*, Jepsen (1930, pp. 525[5]–528) pointed out that it has two characters of *Platychoerops*, the stronger mesostyles and lack of conule on P^4, but otherwise is closer to *Plesiadapis*, and he therefore here and in his later paper (1934) follows Teilhard and makes *Platychoerops* and *Plesiadapis* synonyms. Much discussion is not called for here, but continued use of the name *Plesiadapis* must be explained. Genera are based essentially if not entirely on their genotypes, which are species, in this case *Platychoerops richardsonii* and *Plesiadapis tricuspi-*

[1] Matthew noted that they are separate in some European forms. The separation, better in *Plesiadapis gidleyi* than in *Plesiadapis tricuspidens*, still appears to be a valid character, but of only specific value.

[2] He states that Matthew also distinguished the genera by the absence of a paraconid in *Nothodectes*, but as far as I find Matthew did not give a generic difference in quite this form. It was, as regards the exact point mentioned, a morphological interpretation equally applicable to American and to European forms.

[3] In spite of its being doubly antedated, if this synonymy be accepted, Teilhard continues to call the genus *Plesiadapis*, and Jepsen follows him. This is, of course, invalid.

[4] Jepsen's note (1934, p. 290, footnote 3) might give the impression (not intended by the author) that the genera were separated artificially on the basis of their age in order to preserve *Plesiadapis* from synonymy. They were, in fact, defined by me on numerous definite and specified morphological characters in which the genotypes differ. The difference in age merely gives the then known geological distinction of these natural units, and is not the means of distinguishing them, and the preservation of the name *Plesiadapis* is purely incidental.

[5] On page 525 *Plesiadapis* is inadvertently labeled as a new genus.

dens. To demonstrate their synonymy, it must be held that the differences between these species are of less than generic value. The presence of marginal species, sometimes even difficult to place as to genus, is very common. In ancestral and descendant genera it is not only the rule, but with increasing knowledge is also absolutely inevitable that intermediate species will show gradations between the genera. This fact in itself obviously cannot in any way lessen the distinctiveness of the genotypes and if the latter are, on the whole, so distinct as to warrant generic separation they remain so, no matter how many intermediate structural stages may be found. To maintain any other view would eventuate in considering *Hyracotherium* as synonymous with *Equus.* New discoveries may permit better definition, as they do in this case by showing that the conule of P^4 should not be considered as a generic character of *Plesiadapis,* but even if all the characters of earlier definitions are intermingled in a species this does not in itself make the genera synonymous. In this case such a transition has not been found, although it might well be. Of the seven characters given as distinguishing *Platychoerops* and *Plesiadapis,* which still seem to me of decisive generic value, *Plesiadapis cookei* is like *Platychoerops* in one or two, and otherwise is like *Plesiadapis.* The genera seem to me to be surely distinct, on the most commonly current criteria.[1]

Plesiadapis gidleyi is by far the best known animal of the Tiffany fauna, and of its family, being represented by the whole dentition and many skeletal parts. The morphological description and discussion of affinities have been given separately in the previous paper of this series.

Plesiadapis gidleyi (Matthew, 1917)

Nothodectes gidleyi, Matthew, 1917, p. 832.

Type.—Amer. Mus. No. 17170, upper and lower jaws with most of the dentition.

Paratypes.—Amer. Mus. No. 17171, palate with dentition complete save left P^2.

Amer. Mus. No. 17172, lower jaws with incisors, left P_3 and M_{2-3}, and right M_{1-2}, with parts of maxillae, some upper teeth, and unimportant skeletal fragments.

Important Referred Specimens.—Amer. Mus. No. 17389, left lower jaw with very little worn dentition, lacking only P_2.

Amer. Mus. No. 17372, associated upper and lower milk teeth and first molars.

Amer. Mus. No. 17173, crushed palate with most of cheek teeth.

Amer. Mus. No. 17174, left lower jaw with most of teeth.

Amer. Mus. No. 17200, lower jaws and associated right maxilla, with teeth.

[1] I am strengthened in my belief that this criterion (as to how great a distinction must be to have generic value) is in accordance with current opinion by such cases as the separation of *Parectypodus* from *Ectypodus, Plesiolestes* from *Palaechthon, Teilhardella* from *Eochiromys,* in which Jepsen has established a standard which I accept and by which *Platychoerops* cannot possibly be united with *Plesiadapis.* In further application of such a criterion he recognizes *Chiromyoides,* which is almost certainly closer to *Plesiadapis* than is *Platychoerops.*

Amer. Mus. No. 17388, skull, badly crushed and mixed, with most of cheek dentition, associated with imperfect lower jaws and some skeletal fragments.

Amer. Mus. No. 17379, lower jaws associated with much of skeleton.

HORIZON AND LOCALITY.—Mason Pocket,[1] Tiffany Beds, Colorado.

DIAGNOSIS.—Basal cuspule of lower incisor distinct. P_2 vestigial but apparently always present. P_4 relatively short and wide, no metaconid. Talonids of M_{1-2} considerably wider than trigonids. Hypostylids present on all molars, strong on M_3. Enlarged upper incisor with three apical cusps. Paracone and metacone distinct on P^3 and well separated on P^4. Hypocone region of M^{1-3} without a distinct cusp. Posterointernal part of M^3 widely expanded and basined. Molar mesostyles moderate. Length M_{1-3} (mean of six specimens) 10.5 mm. Other measurements given below.

In uniting the genera *Plesiadapis* and *Nothodectes*, Teilhard (1921), p. 24, added, "Je suis donc convaincu qu 'une comparaison directe des deux formes démontrerait l'identité, non seulement générique, mais spécifique, de *Ples. tricuspidens* et *Noth. Gidleyi.*" Abel (1931, p. 264 and elsewhere) took this prophecy as an accomplished fact, recorded *Plesiadapis tricuspidens* Gervais in the Tiffany, and even reproduced Matthew's figures over this name. With due respect for the synthetic spirit of revision and sympathy with the principle of making taxonomic groups as broad as the facts reasonably allow, in this case it is going too far to suppose that the plesiadapid of southwestern Colorado is exactly the same as its approximately contemporaneous relative of northeastern France. It is rather surprising to find a genus common to the two faunas (generic identity of their animals not being established or probable in any other case), but this is almost certainly correct. The species, however, are very distinct, and not on a priori grounds but on their morphological characters.

The Cernaysian plesiadapids are much larger animals, in the first place. The largest of them are twice the size of *P. gidleyi* and even the specimen figured by Teilhard to show the small extreme in variation (1921, Pl. 1, fig. 5) is one-third larger than the largest specimen of *P. gidleyi*.[2] The very decided difference in mean size, without any overlapping of the size distributions, associated with the widely different proveniences, is in itself a valid specific distinction. In addition there are numerous minor morphological distinctions and while some of these might prove invalid if the original specimens could be compared, it is improbable that they are all illusory. None of the many specimens of *P. gidleyi* has a metaconid on P_4, and the presence of this cusp is given as

[1] One specimen, a single tooth, was found near but not in the Mason Pocket.

[2] I have been unable to find very adequate exact measurements of *T. tricuspidens*, but see below.

typifying *P. tricuspidens* by Teilhard and it is well shown in his figures. *P. tricuspidens* does not appear to have hypostylids, although perhaps they are present and unnoted. Although in *P. tricuspidens* the outer cusp of P^4 has been shown by Teilhard to be divided, nevertheless all the figures and descriptions (including Teilhard's) clearly indicate that the separation is more advanced in *P. gidleyi*. The hypocone of M^{1-2} seems to be a definite cuspule in *P. tricuspidens*, but it is not in *P. gidleyi*, and the posterointernal basin of M^3 seems to be more definite and expanded in the latter. Doubtless some of the numerous other minor and less obvious differences suggested by the published data would be confirmed by direct comparison. The species are surely closely related, but they are even more surely not identical.

P. dubius (Matthew), the first named American species, differs from *P. gidleyi* chiefly in the absence of P_2, longer and more quadrate P_{3-4}, distinct paraconid and metaconid on P_4, and nearly equal width of trigonid and talonid on M_{1-2}. *P. fodinatus* Jepsen also lacks P_2, is said to have a weaker basal cuspule on the lower incisor than in *P. gidleyi*, has relatively narrower P_4 to M_3 than in *P. gidleyi*, lacks the metaconid of P_4 as in that species, and apparently has the trigonid-talonid proportions of M_{1-2} as in *P. dubius*.[1] In the upper teeth, the protoconule appears to be smaller on P^{3-4}, the hypocone more definite on M^2, and the posterointernal expansion of M^3 less in *P. fodinatus* than in *P. gidleyi* but the teeth are closely similar. *P. fodinatus* is slightly but significantly larger than typical *P. gidleyi* or *P. dubius*.

P. cookei Jepsen likewise lacks P_2 and has a simple P_4 as in *P. gidleyi* and, also as in *P. fodinatus*, its lower cheek teeth are less expanded laterally than in *P. gidleyi*. The basal cusp of the lower incisor is lacking. P^4 has paracone and metacone poorly differentiated and lacks the protoconule, a character unique among known species of *Plesiadapis* and suggestive of *Platychoerops*, although the other characters are those of *Plesiadapis*. The upper molars apparently very closely resemble those of *P. gidleyi* except that the inner border of M^1 may be narrower and more rounded. The species is much larger than *P. gidleyi*.

The following table gives the important statistical data on lower teeth of *P. gidleyi*. As all the specimens included are from the Mason Pocket, the sample is probably very homogeneous as to race, but sex and age groups cannot be differentiated. Standard (not Probable) Errors are given:

[1] I take certain striking apparent differences in the contour of M_3 of the figure (Jepsen, 1930, Pl. v, fig. 6) to be due to the combination of a left M_3 with right P_4 to M_1 or to M_2.

Variate	No. of Individuals	Observed Range	Mean	Standard Deviation	Coefficient of Variation
L P_3	11	2.0–2.4	2.20 ± 0.03	0.11 ± 0.02	5.1 ± 1.1
W P_3	11	1.7–2.0	1.77 ± 0.03	0.10 ± 0.02	5.4 ± 1.2
L P_4	11	2.0–2.5	2.27 ± 0.04	0.14 ± 0.03	6.3 ± 1.3
W P_4	11	1.9–2.4	2.09 ± 0.04	0.15 ± 0.03	6.9 ± 1.5
L M_1	12	2.5–3.1	2.84 ± 0.05	0.16 ± 0.03	5.7 ± 1.2
W M_1	11	2.5–3.1	2.67 ± 0.05	0.18 ± 0.04	6.8 ± 1.5
L M_2	12	2.8–3.3	3.13 ± 0.03	0.11 ± 0.02	3.6 ± 0.7
W M_2	11	2.7–3.3	3.04 ± 0.05	0.16 ± 0.03	5.3 ± 1.1
L M_3	11	4.4–4.8	4.63 ± 0.04	0.12 ± 0.03	2.7 ± 0.6
W M_3	8	2.7–3.1	2.87 ± 0.05	0.13 ± 0.03	4.5 ± 1.1

The figures in the following table are the deviation of the particular measurement in the species named from the mean of that measurement in *P. gidleyi*, divided by the standard deviation of the latter. The resulting figure gives a criterion of the significance of the deviation. If this figure is greater than two it is probable and if greater than three it is almost certain that the species differ significantly in this dimension. Significant figures are in bold-face. (Table on p. 7.)

P. gidleyi and *P. dubius* are not distinguishable in size, although they are morphologically. The figures for *P. fodinatus* and *P. cookei* are calculated from Jepsen's published raw data (1930) and show that both species are certainly distinct from *P. gidleyi*. Published measurements of the Cernaysian specimens are extremely scanty. These figures are from raw data published by Lemoine (1878) on a specimen referred to *P. tricuspidens* and the type of *P. recticuspidens*, the latter the smallest Cernaysian specimen (and hence nearest to *P. gidleyi*) that I find recorded in the literature. It is poorly preserved, and the molar widths may have been rather greater than indicated by Lemoine. In any event, it is clear that neither specimen can be conspecific with *P. gidleyi*, even on the basis of size alone. Incidentally, if the variability of *P. tricuspidens* was comparable with that of *P. gidleyi*, the most reason-

Variate	*P. dubius*	*P. fodinatus*	*P. cookei*	*P. tricuspidens*	*P. recticuspidens*
L P_3	...	...	+21.8	....	....
W P_3	...	...	+18.3	....	....
L P_4	+0.9	...	+16.6	+26.6	....
W P_4	+0.1	...	+14.1	+16.1	....
L M_1	+0.4	+5.4	....	....	....
W M_1	−0.9	+1.8	....	....	....
L M_2	+0.6	+5.2	+26.1	+35.2	+11.5
W M_2	−0.9	+1.6	+15.4	+ 9.1	− 3.4
L M_3	...	+7.2	+39.7	+21.4	+ 1.4
W M_3	+1.0	+2.5	+12.5	+10.2	+ 1.0

able assumption, Teilhard cannot be correct in thinking that only one species is present in the Cernaysian, and there must be at least three species and possibly four, as Lemoine thought.

APATEMYIDAE

This family, founded by Matthew (in 1909) but later united by him and by most other students with the Plesiadapidae, has recently been revised and redefined by Jepsen (1934) who has clearly pointed out its many distinctions from the Plesiadapidae. About all the two groups have in common is a basically primate molar structure combined with a diprotodont habitus. The earliest known apatemyid is *Labidolemur*, which was first discovered in the Tiffany fauna but which is now somewhat more satisfactorily known from *L. kayi* Simpson of the Bear Creek, a Tiffany equivalent.

LABIDOLEMUR MATTHEW AND GRANGER, 1921

TYPE.—*L. soricoides* Matthew and Granger.

DISTRIBUTION.—Tiffany and Bear Creek, Colorado and Montana.

DIAGNOSIS.[1]—A typical but primitive apatemyid. Dental formula not determinable but probably $\frac{1\cdot0\cdot2\cdot3}{}$. Crown of enlarged incisor fully enamel covered, and enamel not extending into alveolus (in adult), superolateral edge of crown sharp and crenulated. P_4 with one (*L. kayi*) or two (probably in *L. soricoides*) roots, but in

[1] Much emended after Matthew and Granger, on the basis of subsequent discoveries of related forms and clearer recognition of affinities.

either case less reduced relative to the molars than in later genera. Trigonid of M_1 as wide as talonid and also of about equal length. Talonid of M_3 short and wide, nearly equal to trigonid, no distinct hypoconulid projection or third lobe (*L. kayi*). Mandible relatively slender and elongate for a member of this family.

Aside from its possession of the family characters, fully pointed out by Jepsen, it is very difficult to define this genus adequately, and the real distinctions from it of the more recently named genera *Eochiromys* Teilhard and *Teilhardella* Jepsen are not clear, although there is every reason to suppose that these genera are distinct.

The type material includes only the incisor and M_1 in the jaw, with a separate tooth, possibly P_3, of doubtful association. The latter tooth, apparently found in matrix with the type, is one-rooted and strongly proclivous, but otherwise is not very like P_3 in later genera, as it does not bend down anteriorly and rises to a definite anterior cusp, with anterior and posterior crests, followed by a non-cuspidate heel. There is a strong internal cingulum.

Matthew and Granger doubtfully referred two specimens including M_2 and M_3, but as already pointed out by Jepsen (1934, p. 289), these probably belong to *Ignacius* or *Phenacolemur* and not to *Labidolemur*. They are quite unlike the homologous teeth of *L. kayi*. See also below, *Ignacius*.

Labidolemur soricoides Matthew and Granger, 1921

TYPE.—Amer. Mus. No. 17400, associated right and left lower jaws with incisor and M_1 of each side and doubtfully associated left $?P_3$.

HORIZON AND LOCALITY.—Mason Pocket, Tiffany Beds, Colorado.

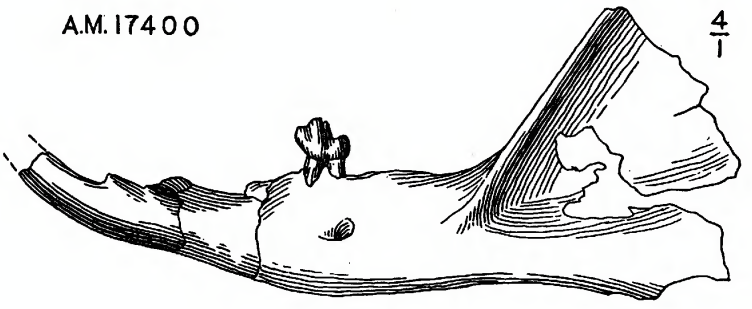

Fig. 1. *Labidolemur soricoides*. Type, Amer. Mus. No. 17400, left lower jaw with incisor and M_1. External view. Four times natural size.

DIAGNOSIS.—Paraconid and anteroexternal cusp of M_1 relatively small, indistinct, and crested. Horizontal ramus slender. Measurements of type as below.

M_{1-3} (approximate, from alveoli of M_{2-3} and crown M_1) 5.5 mm.

M_1 length 1.7, width 1.1 mm.

CARPOLESTIDAE, NEW FAMILY

TYPE.—*Carpolestes* Simpson.

DISTRIBUTION.—Fort Union (Lower Lebo: Torrejon equivalent; "Princeton Quarry Level," Park County, Wyoming: Tiffany equivalent; Bear Creek Beds: Tiffany equivalent) and Tiffany.

DIAGNOSIS.—One enlarged lower incisor, its root not reaching the posterior end of P_4. Intermediate teeth reduced in size and number and becoming one-rooted, button-like vestiges. P_4 much enlarged, with high trenchant blade on which a longitudinal series of cuspules or serrations is developed, heel short and simple and becoming merged with the blade. M_1 with long open trigonid, paraconid distinct and anterior to protoconid. M_{2-3} of plesiadapid or, in less detail, primitive tarsioid type. P^{3-4} becoming large teeth with three longitudinal rows of cuspules, the external row longest and cusps most numerous. Upper molars simple, of primitive tritubercular structure with small but distinct basal hypocone in *Carpolestes*.

The structural series *Elphidotarsius-Carpodaptes-Carpolestes* forms a natural group apparently quite as clearly defined and distinctive as that of the Plesiadapidae and Apatemyidae in Jepsen's redefinitions (1934), and may thus conveniently be regarded as a third family of somewhat analogous adaptive type. The presence of numerous resemblances between the plesiadapids, apatemyids, and carpolestids suggest that they might be separate phyla of a single stock, and hence more properly classified as subfamilies of one family, but this hypothesis must be discarded on present evidence. With few or no exceptions, the resemblances are: (a) shared equally by many other early mammals, hence merely primitive; or (b) shared equally by various early primates, hence evidence of primate relationships and not of relationships between the phyla as such; or (c) shared by numerous possibly related or clearly unrelated groups, as is true of the enlarged incisors, and hence to be considered as purely adaptive characters with no clear significance as to affinities. On the other hand there are important differences that suggest that they may not be derivatives from the same stock at all. For instance, in spite of the many resemblances between plesiadapids and carpolestids, their upper molars differ quite as much (and in analogous ways) as do those of animals belonging to quite different primary subdivisions of the primates, or even quite unrelated ordinally.

The Tiffany fauna contains the middle term of the structural series

represented by the three known genera of this family. *Carpolestes*, which is the most specialized genus and hence is chosen as type of the group, is from beds of nearly the same age in Montana and Wyoming. It differs little from *Carpodaptes*, and may be slightly later (although this seems improbable on other evidence) or belong to a moderately divergent and more progressive line. The most primitive carpolestid is *Elphidotarsius* from a Torrejon equivalent in the Crazy Mountain (Montana) Fort Union. It is decidedly different from the later forms, but in every respect its distinctions are purely primitive and it unquestionably belongs to this line. A more detailed consideration of the structure, evolution, and relationships of this family will be given in the course of a monograph of the Crazy Mountain Field and other work now in progress.

CARPODAPTES MATTHEW AND GRANGER, 1921

TYPE.—*C. aulacodon* Matthew and Granger.

DISTRIBUTION.—Tiffany, Colorado.

DIAGNOSIS.[1]—Dental formula probably $\frac{1 \cdot 1 \cdot 3 \cdot 3}{}$. ?Canine and P_{2-3} reduced, with vertical, cylindrical roots and P_3, at least, with globular, button-like crown. P_4 more enlarged than in *Elphidotarsius*, with four apical cuspules or serrations, an obscure, lower anterior cuspule, and a single talonid cusp, well differentiated from the main blade and lower than the trigonid of M_1. All these cuspules in a straight anteroposterior line. Trigonid blade of M_1 slightly less elongate than in *Carpolestes*. Third lobe of M_3 relatively smaller, less projecting and less asymmetrical than in *Carpolestes*.

Matthew and Granger gave the dental formula as $\frac{?.1 \cdot 4 \cdot 3}{}$, assuming that the large tooth is a canine and that other teeth might occur anterior to it. Jepsen's specimen of *Carpolestes dubius* (Jepsen 1930) showed that this is in fact the most anterior tooth, and he identified it as possibly an incisor, giving the formula (with a query) as $\frac{1 \cdot 0 \cdot 4 \cdot 3}{}$. That the enlarged tooth is an incisor, as Jepsen thought, seems highly probable. It is impossible to determine whether the following tooth is a canine or P_1, but from analogy with the most similar forms it seems slightly more probable that it is the canine, and in any event this legitimate, but purely hypothetical, assumption facilitates comparison with other groups. The formulae of *Carpodaptes* and *Carpolestes* were apparently identical.

The anterior alveolus is so imperfectly preserved in the present specimen that its character is not very clear. In comparison with the better

[1] Modified after Matthew and Granger, for distinction from *Elphidotarsius* and *Carpolestes*, neither of which was known when they wrote.

known *Carpolestes*, especially *Carpolestes dubius* Jepsen, the incisor seems to be slightly less procumbent in *Carpodaptes* and its root to terminate slightly more anteriorly, beneath P_3.

The molar crowns are higher than in *Carpolestes nigridens*, but do not noticeably exceed *Carpolestes dubius* in this respect. The paraconids are distinct on all three molars, apparently a distinction from *Carpolestes dubius* but not from *Carpolestes aquilae* or *nigridens*.

The structure throughout is closely similar to that of *Carpolestes*, which is much better known, and in the several points which validate the distinction of the genera *Carpodaptes* appears to be less specialized.

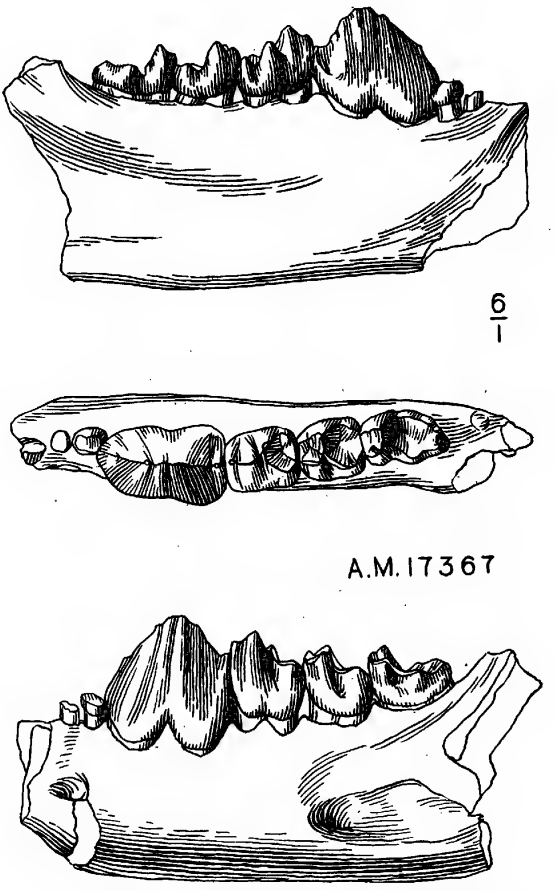

Fig. 2. *Carpodaptes aulacodon*. Type, Amer. Mus. No. 17367, left lower jaw with P_3–M_3. Internal, crown, and external views. Six times natural size.

Carpodaptes aulacodon Matthew and Granger, 1921

TYPE.—Amer. Mus. No. 17367, left lower jaw with P_3–M_3, roots of canine of P_2, and fragment of incisor root.

HORIZON AND LOCALITY.—Mason Pocket, Tiffany Beds, Colorado.

DIAGNOSIS.—Sole known species of genus. Measurements of type below.

M_{1-3}: 4.7 mm.

P_4		M_1		M_2		M_3	
L	W	L	W	L	W	L	W
2.8	1.7	1.4	1.5	1.2	1.4	1.8	1.2

ANAPTOMORPHIDAE

NAVAJOVIUS MATTHEW AND GRANGER, 1921

TYPE.—*N. kohlhaasae* Matthew and Granger.

DISTRIBUTION.—Tiffany, Colorado.

DIAGNOSIS.[1]—Dental formula perhaps $\frac{?\cdot1\cdot3\cdot3}{1\cdot1\cdot3\cdot3}$ (but very doubtful, see below). Enlarged lower incisor with long, straight, spatulate crown. Canine or P_2 erect, one-rooted, with large vertical blade and small heel. P_3 smaller, two-rooted, with similar but lower crown. P_4 large, stout, paraconid not indicated, metaconid barely visible as a rudiment, heel small, partly basined. Molar trigonids triangular in outline, but with anteroexternal angulation. Paraconids very small but distinct, internal. Protoconids and metaconids equal. Talonid basins wide and deep, hypoconulids distinct. M_3 reduced, no third lobe, hypoconulid single. P^4 preceded by three laterally compressed, two-rooted, trenchant teeth, decreasing in size from front to back. P^4 large, transverse, with low but well differentiated protocone, metacone absent or barely incipient. M^{1-2} transverse, of simple tritubercular type with rudimentary basal cingular hypocones, distinct conules, no mesostyle. M^3 reduced.

What appears to be the first lower tooth, presumably an incisor, is preserved separately but with a possible contact on the jaw and probably associated. It is large, although less so than the incisors of *Labidolemur* or *Phenacolemur*, straighter than in those genera, and laterally compressed but with a spatulate, excavated face directed upward and inward (medially) and bounded by sharp longitudinal crests. Matthew and Granger speak of it as being pointed. The tip is not now preserved. This was followed by a much smaller, slightly procumbent tooth with one root, the crown of which is not preserved. The next tooth is vertical,

[1] Somewhat modified after Matthew and Granger.

one-rooted, with a high, very slightly proclivious, blunt spatulate blade followed by a minute heel. It would be natural, from the lower jaw alone, to consider this as the canine, as Matthew and Granger did, but from an upper jaw (not included in their study and presumably not prepared when they wrote) it seems probable that this tooth occluded posterior to the anterior maxillary tooth. If this is correct, it can hardly be the canine, but must be P_2, in spite of its enlargement relative to P_3.

P_3 has two roots and is similar to the preceding tooth save for being much lower. P_4 is a large tooth, rising slightly above M_1. The trigonid is plump and bears a very faint indication of an incipient metaconid. The low heel bears a small basin on the internal side, with two poorly distinguished posterior cuspules.

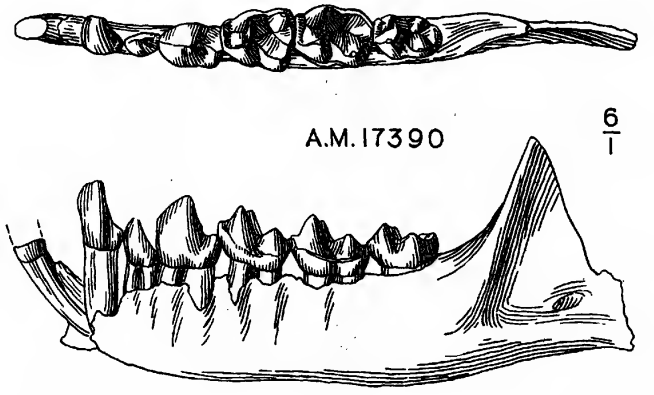

Fig. 3. *Navajovius kohlhaasae.* Type, Amer. Mus. No. 17390, left lower jaw with incisor and P_2–M_3. Crown and external views. Six times natural size.

The molar trigonids are of simple tuberculosectorial type with protoconid and metaconid equal and paraconid very small, anterointernal. The most characteristic modification is that the protoconid-paraconid crest is angulate at the anteroexternal corner of the crown (as in many early primates). The talonids of M_{1-2} are considerably larger than the trigonids and are broadly and deeply basined, with distinct and high hypoconulids in addition to the large, normal hypoconids and entoconids. There is a faint suggestion of twinning of the entoconids. There are moderate external cingula on the talonid of M_1 and talonid and trigonid of M_2, but not on M_3. M_3 is reduced and, although longer than M_{1-2}

relative to its width, has a small and simple heel without third lobe or duplicated cusps.

A specimen (Amer. Mus. No. 17399) evidently cleaned since Matthew and Granger wrote shows the maxillary teeth more completely than does the type. The most anterior tooth (it is not absolutely impossible but is in the highest degree improbable that there was another more anterior in the maxilla) is two-rooted, high, very strongly compressed laterally, and shearing. It has a sharp apex and a convex anterior and straight posterior edge. From its being two-rooted, one would suppose this to be a premolar, but two-rooted canines do occur among primitive mammals; and from its enlargement and general function, its forward position and occlusion apparently even anterior to the caniniform tooth of the lower jaw, and the fact that in the apparently most nearly related animals a premolar is almost invariably lost and the upper canine almost invariably retained, it seems more likely to be a canine.

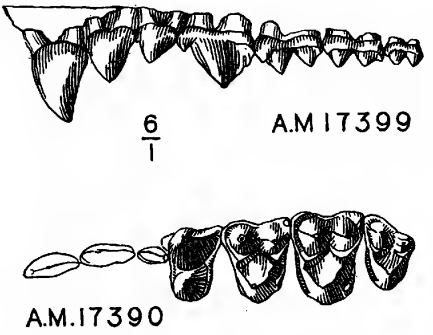

Fig. 4. *Navajovius kohlhaasae.* Amer. Mus. No. 17399, left maxilla with C and P^2–M^3, external view, and the type, Amer. Mus. No. 17390, left P^4–M^3, with canine and P^{2-3} supplied from the other specimen, crown view. Six times natural size.

The following two teeth, probably P^{2-3} in any case, are generally similar but are successively smaller and less compressed. P^4 is nearly as large as M^1 and is fully transverse. The outer wall is high, pointed, and shearing, with small anterior and posterior styles. An incipient metacone may be indicated by a slight deflection of the posterior cutting edge, far from the apex. The protocone is fully distinct and nearly as large as on the molars, but lower relative to the great outer cusp. The posterior cingulum and posterior protocone crest are continuous and tend to form a very small posterointernal basin. There is no posterointernal

cingulum basal to this, and no hypocone. There is a very faint possible indication of a protoconule, but none of a metaconule.

M^{1-2} have paracone, metacone, and protocone about equal in height, small distinct subequal conules, and simple external cingulum all in the usual primitive relationships. There is an anterointernal basal cingulum, not forming a cusp, and a stronger posterointernal cingulum terminating at the inner end in a rudimentary basal cingular hypocone. There are indications of a very feeble ridge from the protocone to the hypocone. M^3 is much reduced in all dimensions, and particularly in the metacone and posterior cingulum.

Matthew and Granger referred this peculiar little animal to the Tarsiidae, implying relationship to the Eocene anaptomorphids which they also placed in that family. This relationship seems most probable on present evidence, although not certain. P^4 and the molars very closely resemble those of *Omomys* and its allies, differing only in minor details of no probable supergeneric significance, but the odd specialization of the more anterior teeth is unlike any other known genus. As this general group in the Eocene is widely variable in its anterior teeth and runs to specializations of a similar, but not identical, nature, this is not strong evidence against relationship. The peculiar lower incisor (which, however, is not certainly associated) is especially striking, but in later anaptomorphids the enlargement of an incisor is common, and the crowns are not known for comparison.

Navajovius kohlhaasae Matthew and Granger, 1921

TYPE.—Amer. Mus. No. 17390, upper and lower jaws, probably of one individual.

PRINCIPAL REFERRED SPECIMEN.—Amer. Mus. No. 17399, upper jaws with all maxillary teeth except left M^{2-3}.

HORIZON AND LOCALITY.—Mason Pocket, Tiffany Beds, Colorado.

DIAGNOSIS.—Sole known species of genus. Measurements of type below.

M^{1-3}: 4.1 mm.

P^4		M^1		M^2		M^3	
L	W	L	W	L	W	L	W
1.6	1.5	1.4	1.7	1.4	1.9	0.9	1.6

Family Uncertain

Phenacolemur Matthew, 1915

Synonym.—*Ignacius* Matthew and Granger, 1921.

Phenacolemur was based on lower jaws from the Sand Coulee and Gray Bull, Lower Eocene, and upper jaw fragments of the same origin were doubtfully referred. *Ignacius* was based on an upper jaw, and *Labidolemur* was described at the same time from a lower jaw. The fragmentary nature of the last two types, with some of the more crucial diagnostic characters missing (as is shown by later discoveries), prevented their clear distinction from each other or from *Phenacolemur*, close resemblance to which was recognized. Jepsen (1934, p. 289) indicated a possible solution of the problem of these various fragmentary dentitions. They can now be sorted out with little possibility of error, and Jepsen's suggestions seem to be fully substantiated.

The attribution by Matthew of upper teeth from the Gray Bull to *Phenacolemur* seems to be beyond any serious question. They are perfectly harmonious with the lower teeth of that genus and occlude exactly with them. The repeated occurrence together of uppers and lowers of this type, here in the Tiffany as well, and the absence in every case of any other known lower teeth with which these characteristic uppers could belong make the association very convincing.

Sorting out the Tiffany specimens, there are four specimens with lower molars which are miniature counterparts of the Lower Eocene *Phenacolemur*. Two are associated with incisors, and two isolated incisors of the same type may thus be added to the group. The upper jaw on which *Ignacius* was based unquestionably belongs with these, not only on the basis of harmony and occlusion and the possibility of association with other known teeth in the collection, but also because the *Ignacius* upper teeth are, like the lowers, exactly like those of Gray Bull *Phenacolemur* in miniature. The two specimens which Matthew and Granger (1921) referred to *Ignacius*, Nos. 17377 and 17498, clearly belong here. The two which they doubtfully referred to *Labidolemur*, Nos. 17401 and 17405, also belong here, the association not having been recognized because of the absence of the characteristic incisors in these specimens and the fact that the teeth present, M_2 and M_3, were unknown in the *Labidolemur* types and also absent in the jaws recognizable as of *Ignacius*.

Labidolemur was compared with *Phenacolemur* by Matthew and Granger and was correctly concluded to be distinct, although the imperfect types and the doubtful inclusion of molars now known actually to belong to *Phenacolemur* made the resemblance seem closer than it is now found to be. The similarity of *Ignacius* was also recognized, but the upper teeth were not compared explicitly (those of Lower Eocene *Phenacolemur* not being surely placed in that genus). The lower teeth of correctly recognized reference were inadequate for proper comparison, and their much smaller size in the Tiffany suggested sharp distinction.

P^3, P^4 to M^2 and the entire lower dentition are now identified in "*Ignacius*" *frugivorus* and they permit detailed comparison with *Phenacolemur*. The general pattern is identical in the two, and the distinctions, aside from size, are all in minor details. These do not seem to warrant generic separation, and the Tiffany species is also placed in *Phenacolemur*.

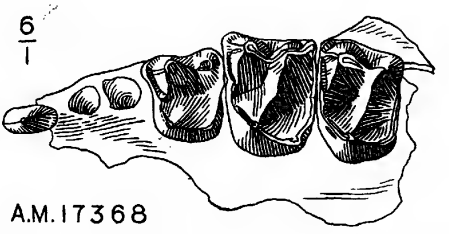

Fig. 5. *Phenacolemur frugivorus*. Type, Amer. Mus. No. 17368, left maxilla with P^2 and P^4–M^2. Crown view. Six times natural size.

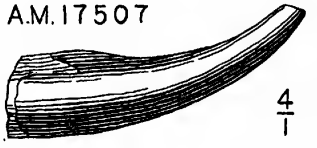

Fig. 6. *Phenacolemur frugivorus*. Amer. Mus. No. 17507, isolated lower incisor. External view. Four times natural size.

The incisor is much enlarged and its straight root is extended horizontally into the mandible to a point (not exactly determinable) under the molars, much as in *Labidolemur*. The crown has the general gracefully curved aspect of that of *Labidolemur*, but is simpler. Its section at the base is smoothly oval and it is modified near the tip only by flattening of the inner, medial, surface and development of a sharp but not elevated angulation below this surface, and another superoexternally. The crown is completely enameled and the enamel does not extend onto

the root. Its posterior margin has a small superoexternal embayment and a larger and more regular medial embayment which follows the mouth of the alveolus, the symphysis here extending forward (between opposite incisors) as a thin film of bone.

The lower cheek dentition is already adequately known in the genus, and the specific distinctions of *P. frugivorus* are noted below.

Despite the loss of all lower teeth between P_4 and the lower incisor, highly probable in *P. frugivorus* and certain in other species, there were

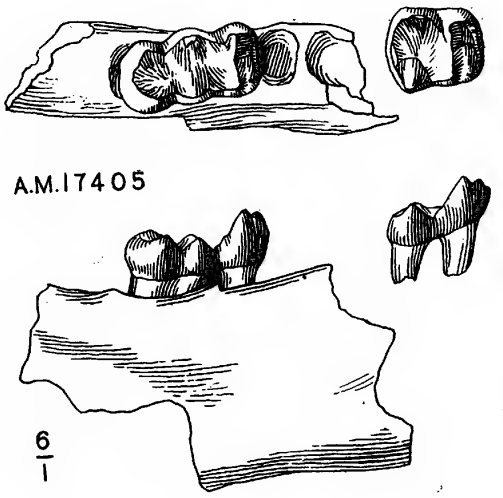

Fig. 7. *Phenacolemur frugivorus*. Amer. Mus. No. 17405, left lower jaw with M_2–M_3 (although detached, M_2 is probably of this individual). Crown and internal views. Six times natural size.

at least two (probably only two) maxillary teeth anterior to P^4. The more anterior, probably P^2, is a small but two-rooted tooth, laterally compressed, rising to a single cusp followed by a non-cuspidate heel. This is followed by a very short diastema. P^3 is implanted by two roots, the posterior slightly larger. Its crown is unknown. P^4 is nearly as large as M^1 and is fully quadrate.[1] Paracone and metacone are distinct, but the metacone is considerably smaller. The protocone is nearly as large relatively as on the molars and is in the extreme anterointernal

[1] P^4 is also known in *Phenacolemur citatus* (in which it is almost identical in structure with that here described) but not hitherto figured or described in this genus.

position. From it a small crest, bearing a minute protoconule, runs to the parastyle, and another runs straight posteriorly, turns at an angle at the posterointernal corner, and continues as the posterior border of the crown, enclosing a large shallow basin, the floor of which slopes to the posterointernal corner. There is no distinct hypocone. An extremely faint ridge from the protocone tip in the direction of the metacone is barely visible on the protocone slope.

M^{1-2}, already described and figured in *Phenacolemur praecox* (Matthew 1915, pp. 480–481), are closely similar to each other, M^2 being slightly smaller. The structure is like that of P^4 but paracone and metacone are nearly equal and more widely separated and a definite crest runs from the protocone to the metacone.

The infraorbital foramen is anterior to the anterior root of P^4, and the zygoma arises principally above M^2, in part also M^3.

Phenacolemur frugivorus (Matthew and Granger, 1921)

Ignacius frugivorus, Matthew and Granger, 1921.

Type.—Amer. Mus. No. 17368, left maxilla with P^2 and P^4–M^2.

Principal Referred Specimens.—Amer. Mus. No. 17408, incisor, P_4, and M_1. Amer. Mus. No. 17405, M_{2-3}.

Horizon and Locality.—Mason Pocket, Tiffany Beds, Colorado.

Diagnosis.—P^4 smaller relative to molars than in other known species. Metacone of P^4 smaller than in *P. praecox*. M^{1-2} angulate in outline, external borders nearly straight. Internal bases not bilobed. Heel of P_4 relatively long, external groove between trigonid and talonid pronounced. Measurements given below.

	P^4		M^1		M^2	
	L	W	L	W	L	W
Type:	1.7	1.9	1.9	2.5	1.7	2.5

	P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W
17408	1.6	1.1	2.0	1.6	...	...	...	...
17405	...	...	...	...	2.0	1.6	2.9	1.6

CARNIVORA

ARCTOCYONIDAE

Thryptacodon australis,[1] new species

TYPE.—Amer. Mus. No. 17384, associated lower jaws, nearly complete, with C–M_3 of both sides except left P_2. Left M^2 possibly associated. Possibly associated skeletal parts.

HORIZON AND LOCALITY.—Mason Pocket, Tiffany Beds, Colorado.

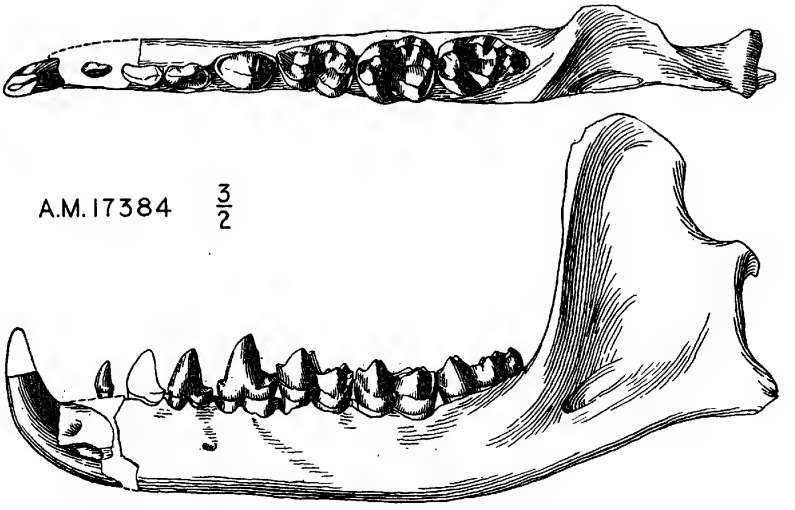

Fig. 8. *Thryptacodon australis.* Type, Amer. Mus. No. 17384, left lower jaw with C, P_1, P_3–M_3, and P_2 supplied in outline from other jaw of same individual. Crown and external views. One and one-half times natural size.

DIAGNOSIS.—M_{1-3} about the same length as in small *T. antiquus*, but anterior teeth slender and less spaced, and whole jaw shorter and much more delicate and slender. Molars narrow and elongate. Paraconids more distinct than typical in *T. antiquus* and metastylids distinctly larger. Talonid of M_3 slightly more elongate, but M_3 as a whole shorter relative to M_2. M^2 with anteroexternal corner more angulate, external margin more sharply and deeply notched, and protoconule stronger.

Thryptacodon antiquus of the Lower Eocene is a highly variable species and some of its extreme variants approach *T. australis* closely,

[1] This hitherto unpublished name appears on the label of the type in Matthew's hand, but no manuscript or notes by him referring to the species can be found and I am therefore forced to assume its authorship.

but the specimens are distinguishable in all cases and there is little doubt that the species are separate.

Skeletal fragments clearly of this species and probably of the type individual were found, including an atlas, humerus crushed but nearly complete, proximal ends of the two ulnae, and the two calcanea, somewhat broken. All these parts except the atlas are known in Lower Eocene *Thryptacodon*, and the present specimens are almost identical with the latter except for their much smaller size (hardly over half linear dimensions) and generally lighter structure. It is suggested that the skeleton was not as large relative to the skull, and certainly not relative to the molars, as in the later forms. The present specimen (assuming the skeletal parts to belong to the type) is, however, young—M_3 is fully erupted but none of the teeth are noticeably worn.

This fine specimen of age comparable to the French Cernaysian permits closer comparison with *Arctocyonides* of the latter, to which *Thryptacodon* has long been known to be closely related, but from which it has never been clearly distinguished. Outstanding distinctions appear to be as follows:

Fig. 9. *Thryptacodon australis*. Amer. Mus. No. 17384, broken left M^2 and fragment of M^3, probably associated with type. Crown view. Twice natural size.

Thryptacodon	*Arctocyonides*
Lower canine very long and procumbent, root extending at least beneath P_2.	Root not extending beneath P_1.
Rudimentary metaconid on P_4.	No metaconid on P_4.
Paraconid well developed on M_1, present but vestigial on M_{2-3}.	Paraconid vestigial on M_1, absent on M_{2-3}.
Paraconid shifts to median position and there becomes vestigial.	Paraconid internal, not median, fusing with metaconid.
Talonid of M_3 elongate, hypoconulid a spur projecting from the basin rim.	Talonid of M_3 short, hypoconulid on basin rim.

These characters show that the genera are distinct, and in view of the general simplicity of pattern and the great amount of demonstrable convergence in animals with similar teeth, even suggest that they may not be very closely related.

Measurements of Type.—M_{1-3}: 20 mm.

M^2 length: 6.7 mm.

P_4		M_1		M_2		M_3	
L	W	L	W	L	W	L	W
5.4	2.8	6.3	4.3	7.0	5.5	6.7	4.6

Chriacus sp. indet.

Amer. Mus. No. 17194 is an isolated upper molar evidently of the genus *Chriacus* and near *C. schlosserianus*, but not that species. The species is doubtless new, but I prefer not to base a name on this poor specimen. It is not closer to the Eocene *C. gallinæ* than to the Paleocene species.

MESONYCHIDAE

?Dissacus sp. indet.

Amer. Mus. No. 17410 is an incomplete premolar, not more exactly identifiable than as probably *Dissacus* but possibly *Pachyaena*, as already stated by Granger (1917, p. 828). This tooth is from a coarse sandstone and is the one exception, mentioned by Granger, to the rule that the Tiffany fossils are from shale or clay.

CONDYLARTHRA

PHENACODONTIDAE

Granger (1917) noted the presence of three species of phenacodonts in this fauna, remarking that the largest is surely *Phenacodus* while the other two, being known from lower teeth only, might belong to *Tetraclænodon*. The latter possibility remains, but their association with an unquestioned *Phenacodus*, the fact that no specimen of *Tetraclænodon* has ever been found at a comparable horizon, and the fact that their structure throughout, while not absolutely decisive, is closest to that of known species of *Phenacodus* make their reference to the latter genus sufficiently probable. Assignment to *Ectocion* is also possible, but careful comparison suggests that they are closer to *Phenacodus*. Gidley suggested the existence at this level of a genus intermediate between *Tetraclænodon*

and *Phenacodus*, but so far as definitely diagnostic characters are shown in the present specimens, they are not intermediate but generically identical with *Phenacodus*.

The three species are all new. The material, although not so good as might be desired, is definable and it seems best to apply names to the species. No others of the same age have been named, with the possible exception of *Ectocion collinus* Russell, from the Paskapoo, based on a broken M^3. This very inadequately known form is distinct from *P. grangeri*. It cannot be compared directly with *P. matthewi* or *P. gidleyi*, but as it seems to be a true *Ectocion*, while the latter are apparently not of that genus, the chance of synonymy is slight. Comparison with the known Clark Fork phenacodonts does not seem closer than with those of the Gray Bull, but is with the more primitive species of these later horizons.

Phenacodus grangeri, new species

TYPE.—Amer. Mus. No. 17185, right maxilla with M^{1-2} and outer half of M^3.

PARATYPES.—Amer. Mus. No. 17188, right P_4.

Amer. Mus. No. 17198, right M_2 and M_3, separate but probably associated.

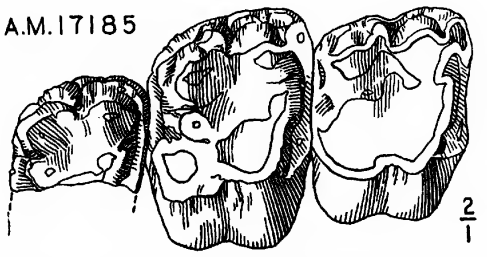

Fig. 10. *Phenacodus grangeri*. Type, Amer. Mus. No. 17185, right M^{1-2} and half of M^3. Crown view. Twice natural size.

Fig. 11. *Phenacodus grangeri*. Paratypes, Amer. Mus. Nos. 17188, 17187, and 17198. A, P_4. B, M_1. C, M_3. (The original of B is of the left side and is reversed in drawing.) Crown views. Twice natural size.

Amer. Mus. No. 17187, left M_1.

HORIZON AND LOCALITY.—Tiffany Beds, Colorado.

DIAGNOSIS.—Comparable to *Phenacodus primævus hemiconus* or to *P. p. intermedius* in size but upper molars more transverse, little reduced. Conules well developed. P_4 rounded-triangular, trigonid low, paraconid strong and simple, entoconid low and indistinct. M_{2-3} closely similar to those of *P. p. intermedius*. Measurements below.

Type: M^{1-3} 29.0 mm.

M^1		M^2		M^3
L	W	L	W	L
9.7	12. 7	10.9	14.4	9.6

Paratypes

P_4		M_1		M_2		M_3	
L	W	L	W	L	W	L	W
10.5	7.8	11.6	9.4	11.2	9.0	11.3	8.2

Phenacodus matthewi, new species

TYPE.—Amer. Mus. No. 17191, right lower jaw with M_{2-3}.

HORIZON AND LOCALITY.—Tiffany Beds, Colorado.

Fig. 12. *Phenacodus matthewi*. Type, Amer. Mus. No. 17191, right M_{2-3}. Crown view. Twice natural size.

DIAGNOSIS.—Intermediate in size between *P. vortmani* and *P. brachypternus*, or slightly nearer the latter. Molars broader than in *brachypternus*. Prominent entostylid on M_{2-3}. Paraconid distinct. Jaw stouter and shallower than in specimens of *vortmani* or *brachypternus* of comparable age. Measurements of type below.

M_2		M_3	
L	W	L	W
7.5	6.9	7.9	5.7

Phenacodus gidleyi, new species

TYPE.—Amer. Mus. No. 17193, right P_4, M_1, and M_3, separate but associated.

HORIZON AND LOCALITY.—Tiffany Beds, Colorado.

DIAGNOSIS.—Molars comparable to *brachypternus* in length, but wider. Heel of M_3 very wide and short, hypoconulid barely projecting. P_4 not elongate, with distinct entoconid. Measurements of type below.

Fig. 13. *Phenacodus gidleyi.* Type, Amer. Mus. No. 17193, right lower teeth. A, P_4. B, M_1. C, M_3. Crown views. Twice natural size.

P_4		M_1		M_3	
L	W	L	W	L	W
7.0	4.8	7.1	5.8	7.8	5.3

Phenacodus, sp. indet.

A single M^3 seems too large for the last two species described, and does not agree with that of *P. grangeri.* It cannot properly be classified at present.

AMBLYPODA

Periptychus superstes Matthew, ex MS., new species

TYPE.—Amer. Mus. No. 17181, associated lower jaws with left P_4–M_3 and right P_4–M_2.

PARATYPES.—Amer. Mus. No. 17183, right ?Dm_4. (Apparently so identified by Matthew. It may be M_1.)

Amer. Mus. No. 17195, left M_3.

Amer. Mus. No. 17184, isolated P^1.

Amer. Mus. No. 17183, various fragments including ?P^4. (So identified by Matthew; might be P^3.)

HORIZON AND LOCALITY.—Tiffany, Colorado.

AUTHOR'S DIAGNOSIS.[1]—"... In size it equals the larger individuals of *rhabdodon* but the heel of M_3 is longer, the inner crescentic cusp of P^4 is larger and more widely separated, the inner cusps of the trigonid of Dp_4 are higher than in Torrejon specimens, subequal in height to the protoconid and more widely separated from it."

REVISER'S DIAGNOSIS.—Overall dimensions of jaw and dentition intermediate between *P. carinidens* and *P. rhabdodon*. Molars close to *rhabdodon* in size and structure, but talonid of M_3 more elongate. Premolars much smaller than in *rhabdodon*, more nearly as in *carinidens* or slightly less transverse.

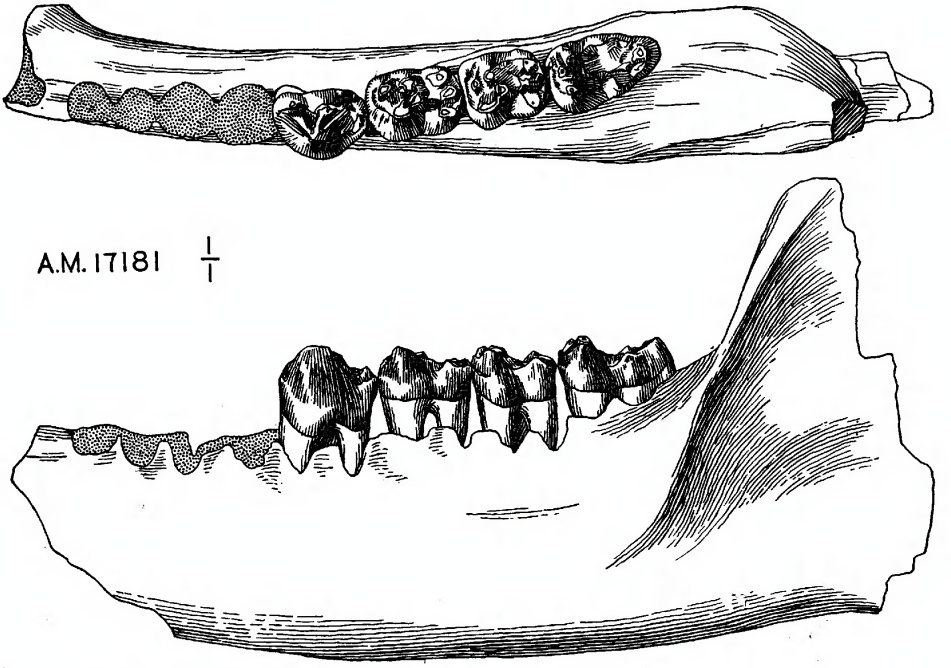

Fig. 14. *Periptychus superstes*. Type, Amer. Mus. No. 17181, left lower jaw with P_4–M_3. Crown and external views. Natural size.

This appears to be the last of the periptychids, none having as yet been found even in the only slightly later Clark Fork. It differs little from the Torrejon species and enters without question into this genus, but is at once distinguishable by the last premolar's being considerably smaller relative to the molar series than in either *P. rhabdodon* or *P. carinidens*, as well as by the other details cited above.

[1] Quoted from Matthew's Puerco-Torrejon memoir. He defines this as a mutation of *P. rhabdodon*. It seems to me as distinct from either *P. rhabdodon* or *P. carinidens* as they are from each other, and I therefore give it full specific rank here.

Measurements of type below.

M_{1-3}: 37.2 mm.

P_4		M_1		M_2		M_3	
L	W	L	W	L	W	L	W
12.3	9.1	11.3	9.2	10.5	9.2	14.6	8.9

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